OBSERVATIONS ON THE PARASITES (HYMENOPTERA, DIPTERA) OF *TRICHOTAPHE LEVISELLA* FYLES (GELECHIIDAE, LEPIDOPTERA) WITH NOTES ON THE HOST[1]

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ABSTRACT

Caterpillars of the aster leaf-tier moth (*Trichotaphe levisella*), believed to winter in the duff under the mats of aster leaves, in May tie the vegetative leaves of *Aster macrophyllus* Linn, in northeastern Minnesota. Sixteen species of hymenopterous parasites and one tachinid fly were observed in caterpillars and chrysalises of this species at Eaglenest Lakes, Minnesota, in 1962–1965. Based on differences in host-parasite relations, there are six categories of the parasites as characterized and exemplified below.

1. Primary, solitary, and endogenic larval parasites in the caterpillar: Braconidae, *Meteorus dimidiatus* (Cresson), *Orgilus indagator* Muesebeck; Ichneumonidae, *Pimplopterus marginatus* (Provancher), *P.* sp. near *parvus* (Cresson), *P.* sp., *Temelucha* sp. near *epagoges* (Cushman), *Scambus pterophori* (Ashmead), *Campoplex* sp.; and Tachinidae, *Lixophaga* sp.
2. Primary, gregarious, ectogenic larval parasites on the caterpillar: Braconidae, *Oncophanes pusillus* Muesebeck.
3. Double-role parasites: as primary, solitary, endoparasites in the caterpillar; and as secondary, solitary, parasites in cocoons of *Temelucha* sp. near *epagoges*: Ichneumonidae, *Scambus tecumseh* Viereck.
4. Primary, solitary, endogenic larvae in the chrysalises: Ichneumonidae, *Phaeogenes* sp.
5. Secondary, solitary, endogenic larvae in cocoons of primary parasites of the caterpillar: Ichneumonidae, *Pimpla* sp., in cocoons of *Temelucha* sp. near *epagoges*; *Gelis* spp., in cocoons of *T.* sp. near *epagoges* and of *Meteorus dimidiatus*; Pteromalidae, *Catolaccus cyanoideus* Burks, in cocoons of *T.* sp. near *epagoges*.
6. Secondary, gregarious, endogenic larva in cocoons of primary parasites of the caterpillar: Eulophidae, *Pediobius sexdentatus* (Girault), in cocoons of *Temelucha* sp. near *epagoges* and of *Pimplopterus* sp.; *Dimmockia pallipes* Muesebeck, in cocoons of *M. dimidiatus*, *Temelucha* sp. near *epagoges*, *P. marginatus*, and *P.* sp. near *parvus*.

INTRODUCTION

Seventeen species of entomophagous parasites were observed associated with the larvae and pupae of the aster leaf-tier moth, *Trichotaphe levisella*, at Eaglenest Lakes, between the towns of Tower and Ely in northeastern Minnesota, in the period from 1962 through 1965. (Both host and parasites were uncommon during the summers of 1966 and 1967, due to the high incidence of parasitism in 1962 to 1965, and to a pathogenic organism that took a high toll of the host caterpillar during a period of heavy rain in late June of 1965.)

Although the investigation was restricted to the months of May to September, it embraced all the aspects of the annual life cycles of the more common parasites and of the host, including deductions concerning the winter stages. Little information can be given about several of the parasites that occurred in very small number, yet their essential roles in relation to the host were determinable.

This article represents a contribution to the bionomics of a natural complex of parasites and host in a habitat that still remains relatively undisturbed. It also presents a classification of the parasites in terms of the types of bionomic relations sustained with the larvae and pupae of the host, *Trichotaphe levisella*.

The parasites are being deposited in the collection of the United States National Museum, Washington, D.C.

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THE ASTER LEAF-TIER, *Trichotaphe levisella* FYLES

Trichotaphe levisella was named and originally described from adult specimens reared by T. W. Fyles at Levis, Quebec, in July, 1902 (Fyles, 1904). Forbes (1923) reported the moth from New York state.

Although several kinds of wild asters (*Aster* spp.) grow commonly in the area of Eaglenest Lakes, only *Aster macrophyllus* Linn. is frequented by *Trichotaphe levisella.* The numerically dominant sterile plants have large cordate leaves borne on petioles about 10 inches long. In many places they grow in extensive stands, and the overlapping leaves form continuous mats that shade the ground and duff beneath. The vegetative plants grow from woody root systems that begin to send up new leaves before mid-May. The leaves become full-grown during the first half of June. *Aster macrophyllus* favors open places on high ground, such as clearings and roadways through woodlands. A relatively small number of fertile plants develop among the abundant vegetative forms. The fertile minority grows about two feet tall, has small pointed leaves, which develop somewhat later than those of the sterile plants, and produces pale purple flowers in mid-summer, but is not utilized in any way by *Trichotaphe levisella.*

The leaf cases

The immature caterpillars of *Trichotaphe levisella* are believed to pass the winter among the aster mats. About the middle of May they form their cases on the leaves of the sterile aster plants. Utilization of the sterile leaves in preference to those of the flowering plants appears to result from the fact that the small caterpillar and the incipient sterile plants develop concurrently. In contrast, the cases do not occur on the small leaves of the fertile flowering plants, probably because their foliage develops decidedly later in the growing season, when the caterpillars are already advanced instars well established in their cases.

When about to form its case, the small larva of *T. levisella* finds the fleshy, tender, immature leaves of the sterile plant still naturally folded loosely along the midrib. The small larva therefore needs only to apply its adhesive silk to the marginal areas of the leaf to prevent the normal unfolding, and thus simultaneously to fashion the leaf case. Here the caterpillar lives singly, scarifying the leaf as it eats the infolded upper cell layer. The fecal pellets mostly accumulate in the petiolar end of the case. Because the leaf continues to grow as the caterpillar grows, additional binding silk must be applied again and again to keep the case intact.

When the caterpillar has pupated and the moth has emerged, the case deteriorates from lack of repair, but still often serves as a shelter for various spiders and as a nest for colonies of small ants. Even while the caterpillar remains immature and active, the roomy lumen of the case was sometimes found to be shared by nymphs and adults of the tingid bug, *Corythuca marmorata* Uhler. This bug not only siphons its food from the leaf tissue of the case wall, but apparently completed its entire life cycle within the case. *C. marmorata* in various stages was taken in the leaf cases between June 29 and August 29.

The larva of Trichotaphe levisella

All the instars of *T. levisella* are slender and very agile and, when the alimentary tract contains fresh tissue of aster leaves, are dark green. The terga of the first seven abdominal segments are marked with a square of four setiferous pinaculi (Figs. 1 and 2).

The life cycle of Trichotaphe levisella

Information pertaining to the life cycle was acquired by analyzing contents of leaf cases taken from aster mats at intervals during the summers of 1962 to 1965. The data so obtained are summarized in sequence as follows.

1. In the period of May 18 to 29, when new foliage of *Aster macrophyllus* was developing from woody roots, the leaf-tier was represented by caterpillars 4 to 16 mm long. The presence of a few individuals of the largest size indicates (1) that *T. levisella* begins its larval life in May, if not in the previous fall, and (2) that a small fraction of the larval population may already have matured and pupated before the samples were collected.

2. In June 11 to 20, the majority of the leaf cases still contined caterpillars 5 to 16 mm long. At the same time, many cases lacked both caterpillars and chrysalids, and showed extensive feeding damage. This condition signified that the caterpillars had matured and pupated in the leaf cases before the material was brought to the laboratory for analysis. The absence of pupal exuviae may mean that the mature chrysalis wriggled to an opening in the leaf case, where the moth emerged from it. Thereupon the pupal exuviae fell to the ground or duff under the aster mat.

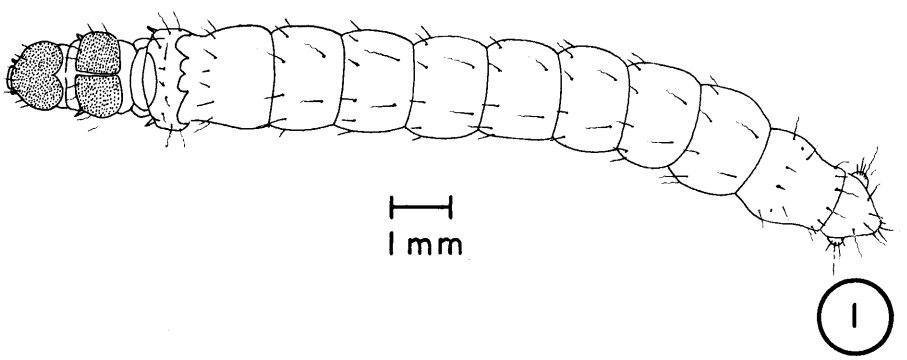

FIGURE 1. Last instar of *Trichotaphe levisella*. Dorsal view. Length 16 mm.

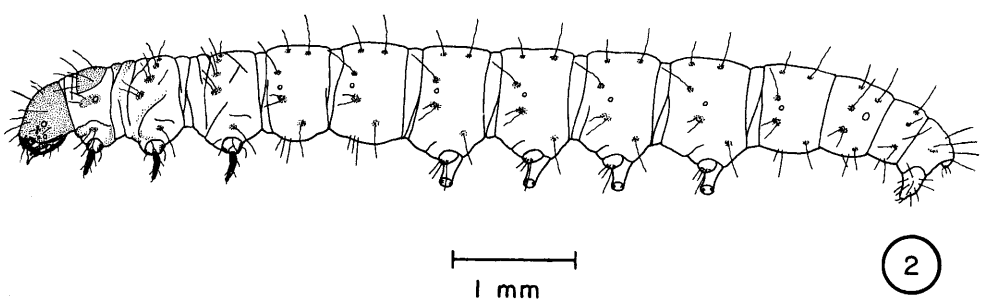

FIGURE 2. Last instar of *Trichotaphe levisella*. Lateral view. Length 16 mm.

3. In the period of June 21 to 30, the small number of caterpillars remaining in the leaf cases sampled measured 6 to 16 mm. A few cases contained living chrysalids in the typical close-fitting white cocoons. The majority of leaf cases had produced full-grown caterpillars and these had chrysalidized and yielded moths before the cases were collected in the field. The absence of empty chrysalids is explained by the same theory proposed above (paragraph 2), that the moth emerged after the chrysalis had wriggled from the leaf case.

4. Of the more than 700 leaf cases processed in the period of July 1 to 10, a few contained chrysalids of *Trichotaphe levisella*. Most cases had deteriorated from lack of repair, because all caterpillars had matured and pupated

or they had been killed by parasites. This condition signifies that (1) the pupal period was approaching its end and (2) the adult moths formed the stage that was active in July and August. In this period, oviposition takes place, and the larvae hatch, then appear to winter as first or second instars.

Summary of the life cycle

This host of many parasites completes one generation in a year. The presence of immature caterpillars of different sizes among the aster mats in the early part of May suggests that this life stage constitutes the wintering form. This view is strengthened by the observations that the common primary parasites appear to winter as first instars in the immature caterpillars. Construction of the leaf cases takes place largely in May. Larval development extends into early July, and chrysalids appear from the last part of June to about mid-July. A series of 55 adult *T. levisella* was reared at Eaglenest Lakes from chrysalids in leaf cases between June 30 and July 22; however, pupation is probably not limited to these dates. The emergence of adults in July and the occurrence of immature caterpillars in mid-May of the next spring are facts which suggest that the moths oviposit in late summer or early fall among the aster mats, but that the small caterpillars, not the eggs, bring *T. levisella* through the winter

PARASITES OF *Trichotaphe levisella*

Seventeen insect parasites that attacked the larval and pupal stages of *Trichotaphe levisella* at Eaglenest Lakes were identified and studied. No attempt was made to consider all the material published on these species. The names of these parasites and of the higher taxonomic groups to which they belong are given below, in the order in which they are described in the following pages.

Order Hymenoptera
- Superfamily Ichneumonoidea
  - Family Braconidae, *Meteorus dimidiatus* (Cresson), *Orgilus indagator* Muesebeck, *Oncophanes pusillus* Muesebeck
  - Family Ichneumonidae, *Pimplopterus marginatus* (Provancher), *P.* sp. near *parvus* (Cresson), *P.* sp., *Temelucha* sp. near *epagoges* Cushman, *Campoplex* sp., *Phaeogenes* sp., *Scambus tecumseh* Viereck, *S. pterophori* (Ashmead), *Pimpla* sp., *Gelis* spp.
- Superfamily Chalcidoidea
  - Family Eulophidae, *Dimmockia pallipes* Muesebeck, *Pediobius sexdentatus* (Girault).
  - Family Pteromalidae, *Catolaccus cyanoideus* Burks

Order Diptera
- Family Tachinidae, *Lixophaga* sp.

Meteorus dimidiatus (*Cresson*), *Braconidae*

Distribution and hosts. *M. dimidiatus* (Fig. 4) has been recorded from the United States and southeastern Canada (Muesebeck and Walkley, 1951) and from British Columbia (Muesebeck, 1958). The microlepidopterans, *Desmia funeralis* (Hübner), *Archips* (*Tortrix*) *pallorana* (Robinson), and *Platynota stultana* Walsingham, and the noctuid *Epizeuxis* sp. are known hosts of *M. dimidiatus* (Muesebeck, 1958, 1967; Muesebeck and Walkley, 1951). At Eaglenest Lakes, *M. dimidiatus* was one of the principal parasites of the aster leaf-tier in all the years of observation, and performed as a solitary, primary, endoparasite of the caterpillar.

Activity of the adult. Ninety-two adults of the parasite, comprising 49 females and 43 males, were reared from their cocoons during June 16 to July 19, in the summers of 1962–1965. The males emerged between June 16 and July 19. I believe that the female cannot enter the sealed leaf case to attack the caterpillar, but that she penetrates the leaf with her long terebra to parasitize the host.

The first instar (Fig. 5). Dissection of numerous aster leaf-tiers disclosed 50 first instars of *M. dimidiatus* between May 23 and June 29, 1963. These parasites inhabited caterpillars 4.0–13 mm long, which I estimate represented third to fifth instars. The first instars of *M. dimidiatus* are readily recognized. They range from 1.2 to 3 mm in length, extremes which indicate the amount of growth made during the first stadium, from hatching to the first ecdysis. The squarish, sclerous, brown dorsal head plate remains essentially unchanged during this period of growth, whereas the trunk, though as wide as the head at hatching, has enlarged to three times that width by ecdysis. The 13 trunk segments are uniform in shape during growth, each tergum divided by a shallow transverse suture into equal anterior and posterior parts. As the larva increases in bulk, the sutures become obscure, and they appear to be obliterated before ecdysis. The prominent tapering fleshy caudal process, or "tail," appears to constitute a character of the genus *Meteorus*, in as much as it also occurs on the first instars of *M. versicolor* Wesmael (Muesebeck, 1918), *M. loxostegei* Viereck (Simmonds, 1948), and *M. indagator* (Riley) (Balduf, 1968). *M. indagator* parasitizes the caterpillar of *Acrobasis rubrifasciella* (Packard) at Eaglenest Lakes. The caudal process of *M. dimidiatus*, at hatching, is about as long as the body, but becomes a mere pointed stub on the full-grown last instar. Similar reductions in size of the caudal process take place on *M. versicolor* (Muesebeck, 1918) and on *M. loxostegei* (Simmonds, 1948).

The young first instars of *M. dimidiatus* are very flexible and active, and therefore strike diverse poses, quickly changing from one form to another. The postures assumed most commonly are: a straight linear form, a double S curve, and a third position in which the "tail" is bent sharply forward and the head is bent backward so that the two ends overlap. But, with growth toward maturity, larvae gradually become less and less mobile and eventually become stolid. The bodies then have a silvery sheen, and their specific gravity is so reduced that they float lightly on water in the dissection dish.

The effect of the first instar on the size of the host larvae is quite marked. Thirty-nine aster leaf-tiers parasitized by first instars of *M. dimidiatus* averaged 8.2 mm, whereas 69 parasite-free larvae measured 8.9 mm in length. All these caterpillars were obtained and processed during May 23 to June 29, 1963.

Three instars were recognized in *Meteorus versicolor* by Muesebeck (1918) and in *M. loxostegei* by Simmonds (1948). In the present study, the last instars of *M. dimidiatus*, as found in the host or discovered as they constructed their cocoons, measured 3.9 to 4.4 mm. The hosts from which these *M. dimidiatus* had emerged varied from 8 to 11 mm in length. Allowing for retardation in growth due to parasitism, the hosts probably were penultimate instars.

When full grown, the larva of *M. dimidiatus* emerges completely from the host. In an hour or two, the margin of the aperture becomes clearly marked with a dark ring of dried blood of the host (Fig. 3). Thus it is easy to determine the precise point from which each parasite larva issued. Table 1 summarizes the locations on the caterpillars' abdomens where 116 parasites were found to have left the host.

Food of the parasite. Microscopic study of leaf-tiers from which the full-grown *M. dimidiatus* larva had emerged showed that the digestive tract, salivary glands, and malpighian tubes of the host remained entire, although depressed. Moreover, the vigorous reactions of the deparasitized host to probing with a needle constituted evidence that the muscular and nervous systems of the host also remained undamaged. Thus, the the parasite must have ingested only the blood and adipose of the caterpillar.

The host caterpillar showed remarkable tenacity of life after emergence of the *M. dimidiatus* larva. In two instances, hosts were observed that still remained alive after the parasite had cocooned, pupated, and emerged as an adult, a trans-

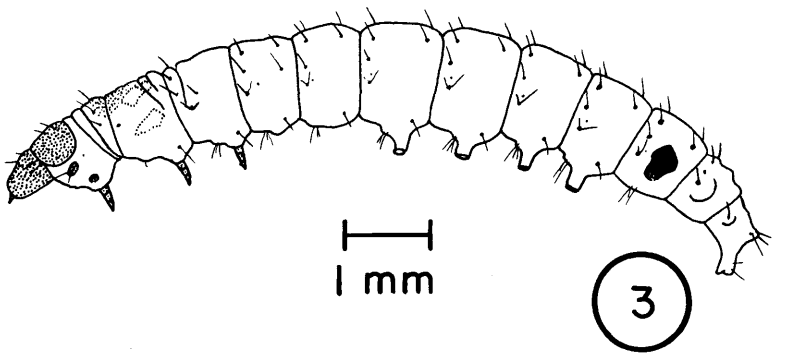

FIGURE 3. Parasitized last instar of *Trichotaphe levisella*. Lateral view. Length 10 mm. Shows emergence hole of *Meteorus dimidiatus* larva on seventh abdominal segment.

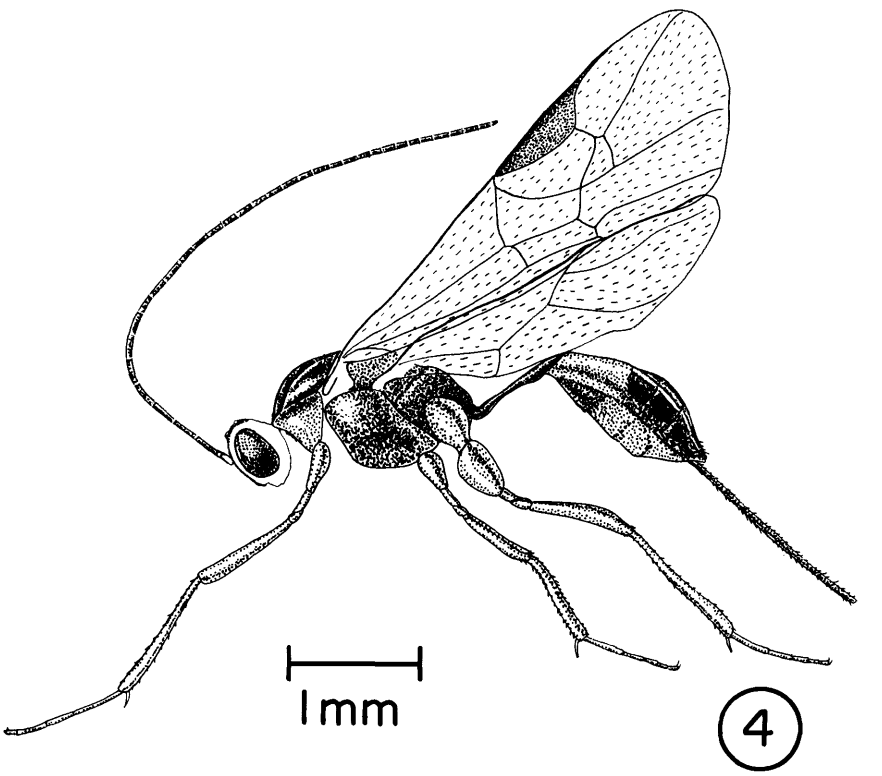

FIGURE 4. Adult of *Meteorus dimidiatus*, female. Body 3.8 mm. long.

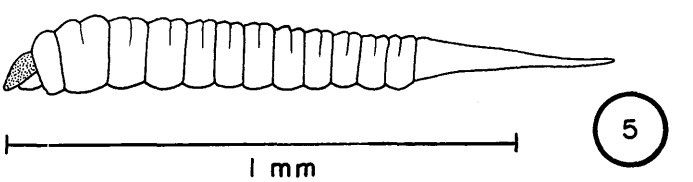

FIGURE 5. First instar of *Meteorus dimidiatus*. Lateral view. Length about 1.2 mm.

formation that required about 10 days. Also the caterpillar commonly retained enough vigor to crawl out of its leaf case after emergence of the parasite larva. However, the host never survived the parasitism of *M. dimidiatus*, but weakened gradually, eventually ceasing to respond to prodding, and was usually found collapsed and dead in its leaf case, only a few millimeters from the cocoon of the parasite.

Cocooning. As soon as it has left its host, the full-grown larva of *M. dimidiatus* begins spinning its cocoon near the inactivated host, a process that requires about two days of continuous work. The completed cocoon is orange-yellow and varies from 3.5 to 4.5 mm in length. The diameter of the bulbous basal part measures about 1.3 mm; the cephalic part narrows gradually toward the apex and terminates as a small but usually distinct knob.

TABLE 1

Loci of emergence

Segment of abdomen	Aspect of segment	Parasites emerged
4th	left pleuron	1
6th	tergum	1
6th	right pleuron	15
6th	left pleuron	10
6–7	conjunctiva	3
7th	tergum	1
7th	sternum	1
7th	right pleuron	45
7th	left pleuron	39

Life cycle of Meteorus dimidiatus. *M. dimidiatus*, like the host, *Trichotaphe levisella*, completes one life cycle in a year at Eaglenest Lakes. The presence of first instars in immature caterpillars in May indicates that parasitization took place in late summer of the previous year, soon after the adult *M. dimidiatus* issued from its cocoon, and that the winter was passed by this instar in the host. Both *M. versicolor* (Muesebeck, 1918) and *M. loxostegei* (Simmonds, 1948) winter as first instars in their larval hosts, *Euproctis chrysorrhoea* and *Loxostege sticticalis*, respectively.

Orgilus indagator *Muesebeck, Braconidae*

Muesebeck (1967) described this new species from 18 adults, of which nine were females and nine were males, which were reared from larvae of *Trichotaphe levisella* at Eaglenest Lakes, Minnesota, in July 1964 and August 1965. With reference to rate of parasitism, this small dark Braconid ranks a close second to *Meteorus dimidiatus* as an enemy of *T. levisella*. Like *M. dimidiatus*, *O. indagator* is a primary, solitary, endoparasite in the caterpillar.

First instar. Although oviposition was not observed, and the eggs were not discovered, the first instars were readily found in the hosts. Two hundred and forty-two first instars were removed from caterpillars of *T. levisella* in the over-all periods of May 23 to July 15, during the years of 1963 to 1965.

Characteristics of this instar (Fig. 6) briefly are: length ranging from 0.5 to 1.3 mm; body laterally C-shaped; scarabaeiform, apodous; dorsal plate of head sclerous, pale brown; trunk 13-segmented, thorax prominent, abdomen tapering moderately, terminating in a short finger-like, caudo-ventrally directed process; exserted caudal vesicle small to prominent, increasing with growth of the instar. When moving in water, this instar normally doubles and extends itself regularly in a jerky sluggish manner, unlike all other parasites of *T. levisella*.

Diapause. With respect to its developmental pattern, the first instar of *O. indagator* appears to be unique among parasites of the aster leaf-tier in that it persists through an unusually long period of time. Instead of advancing promptly to the second instar, as do most hymenopterous parasites, the first instar of *O. indagator* develops or grows slowly, and appears not to attain its advanced, i.e. molting, phase until the host caterpillar is full grown and is thus about to transform to the pupal state. This is not to suggest that the diapausing first instar of *O. indagator* "waits for" the pupation of the host, but rather to say that the instar has lost its ability to effect its own ecdysis, hence has become dependent on the caterpillar to stimulate the molt that terminates the diapause (Balduf, 1963). Cameron (1941) described such an "extremely close relation" between the parasite

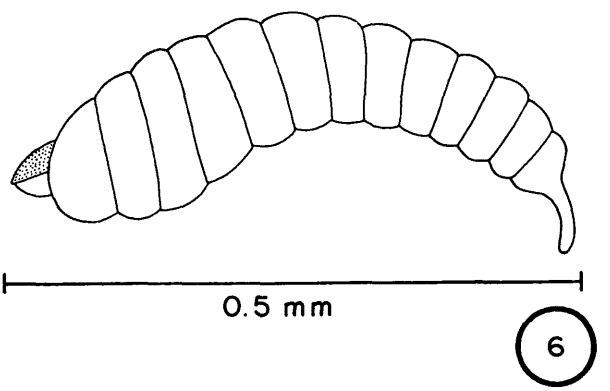

FIGURE 6. First instar of *Orgilus indagator*. Lateral view. Length 0.5 mm.

Opius ilicis Nixon and the holly leaf-miner, *Phytomyza ilicis* Curtis. This relation, states Cameron, is "dependent on the production of certain chemical or physical changes in the composition of the host" that "take place at the time of pupation." The chemical involved in *Trichotaphe levisella*, in my opinion, may be the pupational hormone of the host caterpillar.

The molt of the first instar of *Orgilus indagator* discloses a larva of sack-like form. Juillet (1960) reports and figures five instars for the related *Orgilus obscurator* (Nees). Although parasitized, *T. levisella* spins a cocoon. This is

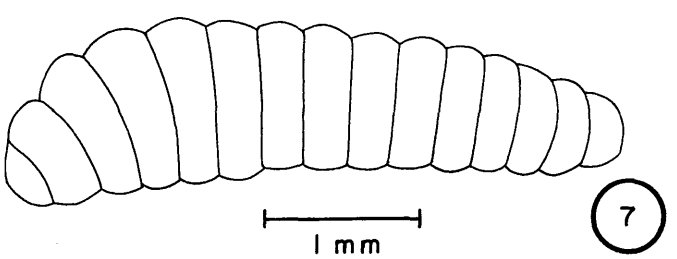

FIGURE 7. Last instar of *Orgilus indagator*. Length about 4 mm.

white, spindle-shaped, 8 to 10 mm long, and concealed in angles of leaf veins or in folds of leaf cases. Now the host is a larviform pupa. Observations on parasitized caterpillars in small vials showed that the advanced instars of *O. indagator* consume the contents of the host in about four days, thereby attaining their full growth. The mature parasite (Fig. 7) then spins its own cocoon, which is elongate-oval firm, and 3 to 4 mm long, within that of the host. After the four or five days required for pupation, the parasite reaches the adult state. The

adult emerges by chewing one round hole simultaneously through both cocoons. Adults reared in the laboratory appeared between June 30 and August 8. Both *O. indagator* and *T. levisella* complete one generation in a year.

Life cycle of Orgilus indagator. Because the young larvae of *Trichotaphe levisella* are believed to make their appearance in late summer, it is probable that they are soon parasitized by *Orgilus indagator,* and that the first instar of the parasite winters in the host. This view is supported by the observation of small (0.5 mm long) first instars of *O. indagator* in *T. levisella* larvae in new leaf cases, as observed during the mid-May following. Similarly, Juillet (1960) found that a congener, *Orgilus obscurator,* mostly winters as first instars (a few as second instars) in small caterpillars of the European pine shoot moth.

Oncophanes pusillus *Muesebeck, Braconidae*

This infrequent primary parasite (Muesebeck, 1967a) on the caterpillar of *Trichotaphe levisella* at Eaglenest Lakes is exceptional in being both external and gregarious as larvae. Thirteen females and one male were reared on July 6 and 7, 1964, from small plumpish lanceolate cocoons that were discovered on June 27 in an aster leaf case. The cocoons had been constructed by larvae that had developed on the surface of the caterpillar. Attached to the leaf surface, the cocoons lay in five groups of one, two, three, and five around a dead collapsed larva of *T. levisella.* The host had been an advanced instar when it was overcome by the external parasitic larvae. A second instance involving *O. pusillus* was discovered on July 4, 1965, on a larva of *T. levisella* 11.5 mm long. The dead collapsing caterpillar bore on its back five small hymenopterous larvae, each 1.5 mm long. By July 8, five flat cocoons had been constructed in depressions on the the leaf within the leaf case. Three adults emerged from these cocoons on July 18.

An European parasite, *Oncophanes lanceolator* (Nees), figured in breaking down the belief held by older entomologists that all parasitic Hymenoptera were endogenic. Ferriere (1922) and his contemporaries established, by rearing several generations, that *O. lanceolator* performed as a gregarious ectoparasite. The host was a leaf-rolling caterpillar, probably *Archips* (*Tortrix*) *sorbiana* Hübner, that infested *Prunus padus* in Switzerland.

The hosts of *Oncophanes* known to Muesebeck (1935) were lepidopterous leaf-rollers and leaf-folders. An exception is *O. betulae* Muesebeck, said to have parasitized the leaf-mining sawfly, *Phyllotoma nemorata* Fallen, on birch trees. Most of the hosts reported for the genus were parasitized by *O. americanus* (Weed).

Pimplopterus marginatus (*Provancher*), *Ichneumonidae*

Heretofore, *P, marginatus* (Fig. 8) was known from West Virginia and from along the Atlantic Coast north to Quebec and Ontario, the single recorded host being the aster leaf-tier, *Trichotaphe levisella* (Townes and Townes, 1951). *T. levisella* also was the host from which *P. marginatus* was reared at Eaglenest Lakes, where the latter performed as a primary, solitary, endoparasite in the caterpillar. *Pimplopterus* sp. near *parvus* and *P.* species also maintain these relations with the caterpillar of *T. levisella.*

First instar. What are believed to be the first instars of *P. marginatus,* or possibly of the other two species of *Pimplopterus,* were found in *T. levisella* caterpillars 5 to 11 mm long, and taken between June 7 and 23 in several different years. The instars ranged from 0.9 to 3.5 mm in length. Seen in profile, the arcuate body is tallest in the thoracic region, due to a dorsal bulge formed by a pair of tracheal reservoirs. The somewhat elongate head is topped with a pale-brown sclerous plate that curves downward, beak-like, at the apex. The abdomen narrows caudad and terminates in a caudal vesicle. Below the vesicle is a short tapering, oblique caudal process.

Full-grown larvae. A few full-grown larvae of *Pimplopterous marginatus* were removed from host leaf-tiers that measured 14 to 15 mm long, i.e. probably

retarded final instars. Other *Pimplopterus* larvae of like form and size (Fig. 9), taken between June 21 and July 23 while spinning cocoons, varied from 6.9 to 8.2 mm long. Some of these were probably full-grown larvae of *P.* sp. near *parvus* and *P.* sp. described below. Due to its large size relative to the host, the emerging mature parasite larva fragments the cuticle of the host and crumples the pieces in a mass that usually becomes superficially entangled in the outer meshes of the cocoons. The cocoons in the three forms of *Pimplopterus* that parasitize the leaftier, *T. levisella,* are similar, all being dark brown, plain, and cylindrical, with

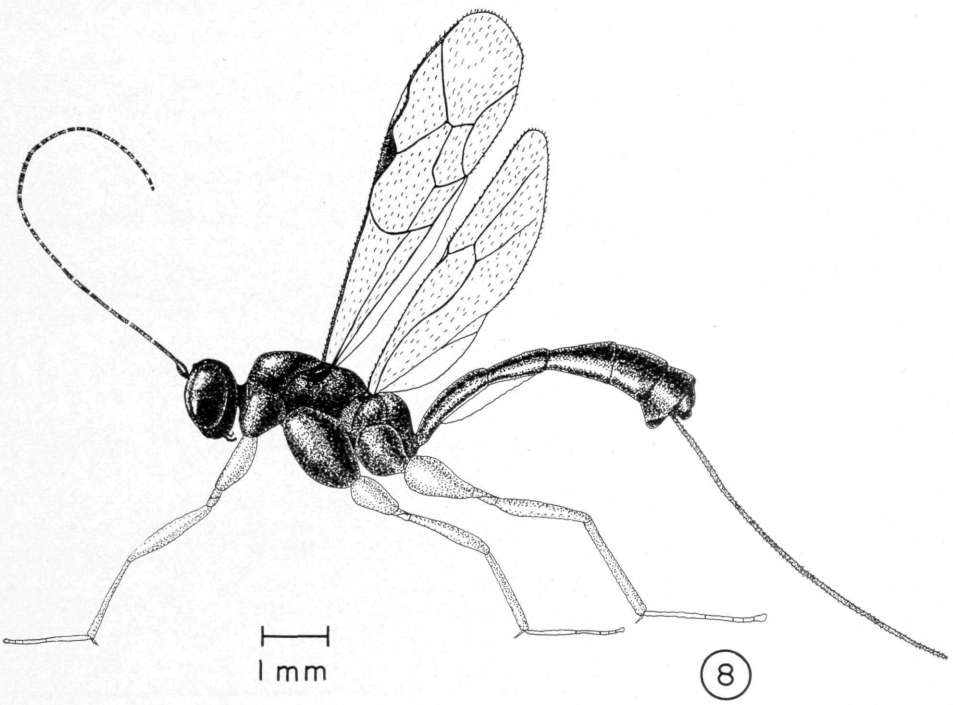

FIGURE 8. Adult of *Pimplopterus marginatus,* female. Length of body about 8 mm.

bluntly rounded ends, and enclosed in folds of thin gray webbing within the leaf cases. Most of the cocoons measure about 8 x 2 mm. Exit holes made by the emerging adult *Pimplopterus* are subcephalic in position.

Life cycle. Emergence of 13 adult *P. marginatus,* all of which were female, from cocoons in cages, took place between July 2 and 30, 1961 to 1965. One larva found constructing its cocoon on June 30, 1962, developed as an adult female on July 13. Transformation required 13 days. The season and activity of

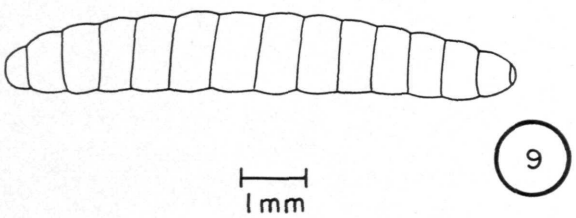

FIGURE 9. Full-grown larva of *Pimplopterus marginatus.* Length about 8 mm.

oviposition were not observed. However, emergence of the adults from their cocoons during July suggests that eggs were laid late in the same summer in small larvae of *T. levisella*. Hence the parasite may winter as an early instar within the host. Development of the larvae then follows in May to July. One generation per year is indicated.

Pimplopterus *sp. near* parvus (*Cresson*), *Ichneumonidae*

Eight adults of *P.* sp. near *parvus*, all females, were reared at Eaglenest Lakes. Six of these emerged during the period of June 18 to July 13, 1963, and two on July 7 and 8 in 1964. The full-grown larva abandons the nearly mature-sized leaf-tier and constructs a cylindrical brown cocoon, about 7.5 x 2 mm, in the leaf case of the host. A thin grayish web envelops the cocoon. The first instars were not distinguishable from those of *P. marginatus* and *P. species*. Two full-grown larvae discovered in the process of cocooning transformed to adults in 12 days, emerging on June 28 and July 10, 1963.

Pimplopterus *species, Ichneumonidae*

This unnamed third species of *Pimplopterus* obtained from the aster leaf-tier is represented by two females. One emerged on June 30, 1962, the other on July 20, 1965. The cocoons are very similar in size, form, and color to those of *P. marginatus* and *P.* species near *parvus*. In one instance, the host larva was only 10 mm long when the mature parasite larva broke out of it. Construction of the parasite cocoon and transformation to the adult stage required about 14 days.

The movements of the host caterpillar observed just before emergence of the large larva of *Pimplopterus* sp. from the caterpillar were probably caused by wriggling of the internal parasite larva. Hence, it is probable that the host was dead at this time. This relationship obtains where the almost-mature parasite is large relative to the host and needs to consume all the ingestible substance of the host in order to mature. But when the parasite is relatively small, e.g. *Meteorus dimidiatus*, the host may remain alive for a week or more after the larva emerges.

Temelucha *species near* epagoges *Cushman, Ichneumonidae*

Fifty-nine adults of this species, comprising 35 females and 24 males, were reared at Eaglenest Lakes in the summers of 1962 to 1965. Emergence from the cocoons took place between July 8 and 27. Numerically this species ranked third in abundance, after *Orgilus indagator* and *Meteorus dimidiatus*, as a parasite of *Trichotaphe levisella*. It performed as a primary, solitary, endoparasite in the caterpillar.

First instars. The living first instars (Fig. 10) vary, with age, from 1.35 to 3.4 mm in length. Other characteristics of this instar, briefly are: dorsal plate of head quadrate, sclerous, brown; general form of body similar to the first larva of *Meteorus dimidiatus*, but trunk segments lacking the superficial annulations; caudal process distinctive in being laterally compressed, with an angular, dorsobasal notch and a corresponding ventral bulge, its apical part being arched, tapering, and flexible.

Seventeen such first instars were removed from caterpillars of *Trichotaphe levisella*, 3.5 to 11 mm long, between May 26 and June 13, 1964, and similar numbers were obtained in 1965. The full-grown parasite larvae, each with a rudimentary caudal process, have a simple sack-like form (Fig. 11) and average about 5 mm long. They attain their maturity in host caterpillars 12 to 14 mm long, which are probably last instars (full-grown, parasite-free caterpillars reach lengths of about 16 mm). The fragmented cuticle, all that remains of the host, is attached lightly to a side or end of the cocoon of the parasite.

The cocoon of *Temelucha* is cylindrical, moderately rounded at the ends, and enclosed in a thin web of grayish-white silk. It is usually dark brown, and about 4 to 6 by 1.5 mm in dimensions. It can be distinguished from the cocoon of

Pimplopterus by the definite, although sometimes faint, transverse band of grayish silk around the median fourth. A total of 103 whole cocoons were discovered in leaf-cases of *Trichotaphe levisella* in the years 1963 to 1965. Like those of other primary parasites described here, the cocoons of *Temelucha* are attacked by hyperparasitic chalcidoids and ichneumonids, the latter being mostly Gelinae.

The related species, *Temelucha* (*Cremastus*) *interruptor* (Gravenhorst), a parasite of the European pine shoot moth, was investigated by Juillet (1960). If close relatives have similar life cycles, *Temelucha* near *epagoges* may be expected to parasitize the small *Trichotaphe levisella* caterpillars late in the summer, and to pass the winter as first instars in the host. Confirming this pattern in part, I have found small first instars of *Temelucha* near *epogoges* in overwintered *Trichotaphe levisella* in late May, when work on this parasite was resumed.

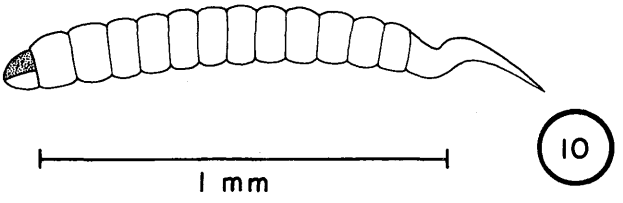

FIGURE 10. First instar of *Temelucha* sp. nr. *epagoges*. Lateral view. Length 1.35 mm.

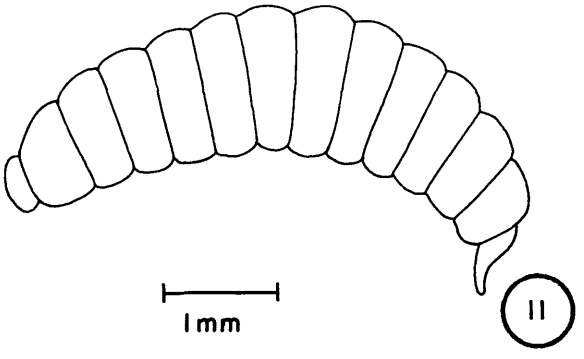

FIGURE 11. Full-grown larva of *Temelucha* sp. nr. *epagoges*. Length about 5 mm.

Campoplex *sp.*, *Ichneumonidae*

A female of *Campoplex* sp. emerged on June 29, 1962, from its cocoon, which was discovered on June 26, in an aster leaf tied by the caterpillar of *Trichotaphe levisella*. The cocoon was robust, 7 x 2.5 mm in dimensions, oval and off-white, with a cover of tangled silk. Held in this tangle was the head capsule of an approximately half-grown larva of *T. levisella*. The *Campoplex* had developed as a primary parasite of the aster leaf-tier, but whether externally or internally was not learned.

Phaeogenes *sp.*, *Ichneumonidae*

Two males of *Phaeogenes* sp. were acquired at Eaglenest Lakes. They developed as primary, solitary, endoparasites in chrysalids of *Trichotaphe levisella*, that remained in their leaf cases. Both *Phaeogenes* issued through the cephalic ends of the hosts, one on July 23, 1963, the other on July 14, 1965.

Scambus tecumseh *Viereck, Ichneumonidae*

Eight adults of *S. tecumseh* developed in leaf cases of *Trichotaphe levisella*. Four males appeared in the period of July 10 to 19, 1964; two males and two females appeared between July 12 and 24, 1965.

An unusual bionomic feature of *S. tecumseh* is that it sustained two kinds of relations with the host. The larvae of five individuals attacked caterpillars of *T. levisella* in aster leaf cases. When the full-grown *Scambus* larva broke out of the caterpillar, it constructed a cocoon in the leaf case, from which cocoon the adult *S. tecumseh* emerged. Hence, this relation of the parasite may be summarized as primary, solitary, and endogenic in the caterpillar of *T. levisella*.

By contrast, three adults of *S. tecumseh* developed, not directly in caterpillars of *Trichotaphe levisella*, but each in a separate cocoon of *Temelucha* near *epagoges*. The *Temelucha* functioned as a primary, solitary endoparasite in the *Trichotaphe levisella* caterpillar, and made its cocoon in the leaf case. Soon thereafter, the parent female of *S. tecumseh* parasitized the *Temelucha* pupa in the cocoon, and its larva developed at the expense of the *Temelucha* pupa. The adult progeny of *S. tecumseh* emerged from the cocoon after the few days required for pupation. Because *S. tecumseh* attacked the pupa of *Temelucha*, instead of the caterpillar of *Trichotaphe levisella*, it performed as a secondary parasite, i.e. its host was itself a parasite. Although it fed externally on the pupa, the *S. tecumseh* larva is nevertheless regarded as endoparasitic, because it lived concealed within the cocoon of *Temelucha*.

Scambus pterophori (*Ashmead*), *Ichneumonidae*

On July 9, 1964, a slender white pupa of this *Scambus* was found in a loose white cocoon in a leaf-case of *Trichotaphe levisella*. The adult *S. pterophori* appeared from the cocoon on July 12, 1964. It appears to have developed as a primary parasite in the caterpillar of the case-maker.

Pimpla *sp., Ichneumonidae*

A banded cocoon of *Temelucha* near *epagoges* was discovered in a leaf case of *Trichotaphe levisella* on July 9, 1964. A male of *Pimpla* sp. developed here as a secondary parasite of *T. levisella*, through the cocoon of *Temelucha* near *epagoges*, itself a parasite in the leaf-tier.

Gelis *spp., Ichneumonidae*

A total of five apterous adults of *Gelis* spp., one male and four females, were obtained from *Trichotaphe levisella* in 1963 to 1965. It was not determined how many and which species of *Gelis* were involved. Two females issued from cocoons of *Meteorus dimidiatus*, one on July 17, 1964, and one on August 2, 1965. Three *Gelis* emerged from cocoons of *Temelucha* near *epagoges*; a male on July 10, 1964, one female on August 7, 1963 and another female on July 27, 1965. Because *M. dimidiatus* and *Temelucha* near *epagoges* have roles as primary parasites in caterpillars of *Trichotaphe levisella*, all the five *Gelis* that emerged from cocoons of *Meteorus* and *Temelucha* performed as secondary or hyperparasites.

Dimmockia pallipes *Muesebeck, Eulophidae*

Dimmockia pallipes was by far the most numerous of all the hyperparasites found associated with *Trichotaphe levisella* at Eaglenest Lakes. Its role was that of a gregarious, secondary parasite in the cocoons of four species of primary parasites of *T. levisella* caterpillars, namely *Meteorus dimidiatus*, *Temelucha* near *epagoges*, and probably two species of *Pimplopterus*, *P. marginatus*, and *P.* sp. near *parvus*. The cocoons of all these primary parasites occurred within the leaf cases.

Muesebeck (1927) described *D. pallipes* (Fig. 12) using adults obtained from cocoons of *Apanteles melanoscelus* (Ratzeburg), a braconid parasite in larvae of the gypsy moth. The Eaglenest sample of 211 adult *D. pallipes* was reared in the over-all period of July 4 to 26, 1962 to 1965. They developed in 33 cocoons, 31 of which were spun by the relatively numerous *Meteorus* and *Temelucha*. Only two *D. pallipes* emerged from cocoons of the *Pimplopterus* species. Although cocoons of *Orgilus indagator* are relatively common, they appear to escape attack by *D. pallipes* because of their obscure position in the folds of the leaf case within the cocoon of *Trichotaphe levisella*.

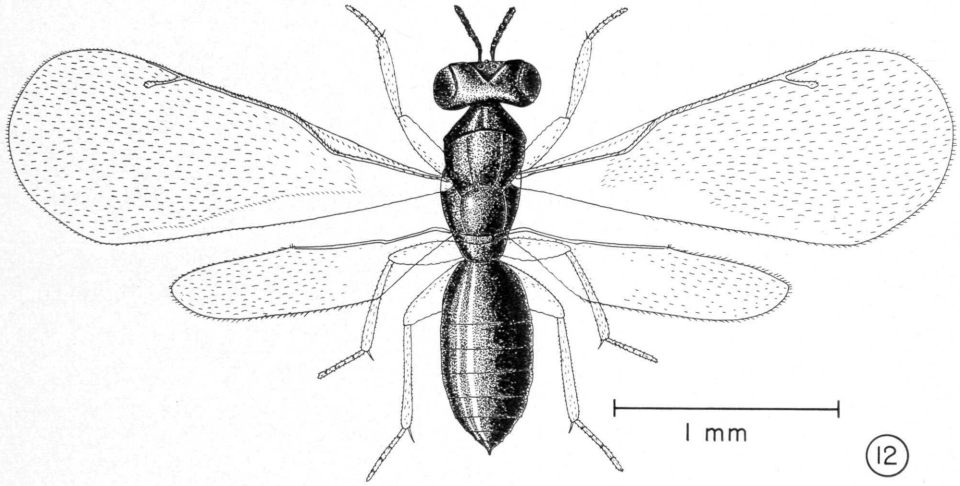

FIGURE 12. Adult of *Dimmockia pallipes*, female. Length 1.8 mm.

This collection of *D. pallipes* comprised 183 females and 28 males, a sex ratio of 6.5 to 1. The number of individuals of *D. pallipes* that developed in each instance was roughly proportional to the volume of the cocoon. Specifically, two cocoons of *Pimplopterus* spp., which were about 8 mm long, yielded *D. pallipes* at rates of 12 females to one male and 12 females to 2 males. The cocoons of *Temelucha* measured 5.6 to 6 mm in length, and produced 5 to 11 females in contrast to 1 or 0 males. *Meteorus* spun cocoons only 4 to 5 mm long, which gave rise to 3 to 8 females and to 1 to 0 males each. With few exceptions, each of the above cocoons parasitized by *D. pallipes* contained only one male.

Adults of all *D. pallipes* observed at Eaglenest Lakes issued from the cocoon by way of a single small hole. This opening varied widely as to its location on the cocoon, from terminal to subterminal to lateral. Casual observations have led me to suspect that the single precocious male prepared the exit and that all the females subsequently issued through that same single opening.

Pediobius sexdentatus (*Girault*), *Eulophidae*

The role of *Pediobius sexdentatus* in the life of *Trichotaphe levisella* was revealed in two instances observed at Eaglenest Lakes. In the first, a banded cocoon of *Temelucha* sp. near *epagoges* was found on July 18, 1965, in an aster leaf case tied by a *T. levisella* caterpillar. Eighteen days later, on August 5, five adults (comprising 4 females and one male) of *P. sexdentatus* emerged through a single hole chewed in the side of the banded *Temelucha* cocoon.

In the second instance, a dead female of *P. sexdentatus* was discovered on July 16, 1965. The terebra of the ovipositor had been inserted into an end of a

cocoon of *Pimplopterus* sp. in an obvious attempt to parasitize the pupa within. However, the attempt had failed, for the cocoon yielded an adult *Pimplopterus* on July 24. Moreover, the effort also resulted in the death of the *P. sexdentatus*, because of its inability to extricate its terebra from the host cocoon. This instance shows also that *P. sexdentatus*, only 1.5 mm long, does not pierce the leaf with the ovipositor in order to parasitize the host cocoon within, but enters the case bodily to do so. In this instance, entrance to the leaf case was almost certainly gained by *Pediobius* through breaks in the case wall that developed after the caterpillar was killed by *Pimplopterus*. The leaf cases fall into disrepair after death of the case-maker. The above two instances show that *Pediobius sexdentatus* performed as a gregarious hyperparasite of the *Trichotaphe levisella* caterpillar through the pupae of the primary parasites *Temelucha* and *Pimplopterus* in their cocoons.

Catolaccus cyanoideus *Burks*, *Pteromalidae*

A single female of *C. cyanoideus* was obtained at Eaglenest Lakes. A case of the aster leaf-tier, *Trichotaphe levisella*, was observed to contain a cocoon of the internal parasite *Temelucha* sp. near *epagoges* on July 9, 1963. Subsequently a parent female of *C. cyanoideus* parasitized the *Temelucha* cocoon. A daughter *C. cyanoideus* developed in the cocoon and emerged on July 23, 1963. These facts show that the daughter performed in the capacity of a solitary parasite, i.e. hyperparasite, of the aster leaf-tier through the cocoon of the parasite *Temelucha* sp. near *epagoges*.

Lixophaga *sp.*, *Tachinidae*, *Diptera*

The tachinid fly, *Lixophaga* sp. was one of the more numerous parasites of the aster leaf-tier at Eaglenest Lakes. However, only three adults were acquired; a male on July 12, 1961, one female on July 9, 1961, and another female on July 17, 1963. The latter female was reared from its puparium. The maggot, or larva, had performed as a solitary endoparasite in a caterpillar of *Trichotaphe levisella*. A total of 72 maggots, embracing all the three instars, were taken between May 20, when dissections were begun, and June 29, 1961 to 1965.

The first instar of *Lixophaga* begins its life as a free, mobile maggot in the host caterpillar. Such unattached maggots, 0.6 to 1 mm long, were obtained by dissection of caterpillars 6 to 9 mm in length, from May 20 until June 7, 1963, and on June 5, 1964. Somewhat later in the same period, other maggots that measured 1–1.9 mm long were observed, attached by a funnel-like caudal mechanism to the inner surface of hosts 9–13 mm long. As seen from outside through the host cuticle, the apex of the funnel appeared as a heavy black ring with a central respirative aperture. The larger membranous apex of the funnel enveloped the caudal respiratory end of the parasite. The maggots were attached variously to the dorsal, lateral, and ventral aspects of the meso- and meta-thorax, and to the anterior abdominal segments.

A full-grown maggot, found in the act of emerging from the host, had anchored itself by means of its tracheal funnel while breaking the cuticle of the caterpillar with its mouth hooks. Several full-grown maggots newly emerged from their hosts were taken during the period of June 25 to 29, 1963. They measured about 4 mm long when at rest, but, when creeping, stretched to lengths of 6 mm.

In order to obtain a sample of puparia of *Lixophaga* sp., 245 leaf cases from *Aster macrophyllus* were confined in paper bags on June 28, 1963. On this date the maggots were approaching their maturity; some had already emerged from the caterpillars of *Trichotaphe levisella* and pupariated in the cases. Ten puparia resulted from the 245 cases; some remained in the cases, while other maggots left them and pupariated among the refuse in the bags. Transformation from maggot to puparium took place between July 3 and 11. Only one adult fly emerged from the ten individuals, this on July 14. It is probable that failure to obtain more

adults was due to ill-adapted rearing methods. The acquisition of these adults between July 9 and 17 suggests that mid-July is the natural period of emergence of the adults from the puparia. An effort to obtain additional *Lixophaga* in 1965 was thwarted by an undetermined pathogen, which flourished on *Trichotaphe levisella* during a period of heavy rains. As a consequence, the populations of *T. levisella* and *Lixophaga*, as well as those of the other parasites, were greatly reduced in 1965.

Life Cycle. The occurrence of first instar maggots of *Lixophaga* sp. in immature caterpillars of *T. levisella* in May, and the emergence of the adult fly in mid-July, indicate that this parasitization of small caterpillars takes place in late summer. These facts indicate further that the first instar parasite winters in the caterpillar. The maggots become full grown and emerge from the host in late June and early July. Pupariation follows at once after emergence, and the adult flies leave the puparia in mid-summer.

Phagocytes? *on* Lixophaga *larvae.* A small percent of the endoparasitic maggots of *Lixophaga* taken from the caterpillars of *Trichotaphe* were affected by what appeared to be phagocytic blood cells of the host. In the period of June 7 to 29, 1963, five dead maggots 0.8 to 1.9 mm long were found to be enveloped to various extents by a whitish substance of granular jelly-like appearance. All the victims appeared to be first instars. One caterpillar contained three *Lixophaga* maggots, 1, 2.5, and 3 mm long. Only the smallest, surely a first instar, bore the granular substance. The large majority of *Lixophaga* parasites found in the caterpillar were alive and healthy. It is of interest also that no larvae of the several primary hymenopterous endoparasites of the *Trichotaphe* caterpillars were thus affected.

Multiparasitism. As observed in *Trichotaphe levisella*, multiparasitism means that the larvae of two distinct species of primary parasites occur simultaneously in one individual of the host caterpillar. In all the instances of multiparasitism observed in this study, each species of parasite seems to have been represented by a single first instar. Hence, the term multiparasitism does not apply to the secondary gregarious species, e.g. the eulophid chalcids, *Pediobius* and *Dimmockia*, from cocoons of *Meteorus* and *Pimplopterus*.

The phenomenon of multiparasitism was exemplified in the present complex of parasites attacking the parasitic species as follows: (1) larvae of *Temelucha* and *Lixophaga*, (2) larvae of *Meteorus* and *Lixophaga*, (3) larvae of *Orgilus* and *Lixophaga*, and (4) larvae of *Meteorus* and *Orgilus*.

Such multiparasitism may be expected to exist in situations where the several parasitic species involved (1) develop simultaneously in a given area, and (2) occur in numbers sufficient to increase the chances of the two-fold attacks.

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REFERENCES CITED

Balduf, W. V. 1963. A distinct type of host-parasite relation among insects. Ann. Ent. Soc. Amer. 56: 386–391.

———. 1968. Bionomic notes on the insect parasites (Hym., Dip.) of the alnus case-maker, *Acrobasis rubrifasciella* (Packard) (Phycitidae, Lep.). Ent. Soc. Amer. Ann. 61: 463–476.

Cameron, Ewen. 1941. The biology and post-embryonic development of *Opius ilicis* n. sp., a parasite of the holly leaf-miner (*Phytomyza ilicis* Curt.). Parasitology 33: 8–39.

Ferriere, Ch. 1922. Le parasitisme externe des *Oncophanes* (braconides). Schweizer entomolog. Anz., Dubendorf-Zurich, 1: 3–4 (only vols. 1–5 published). (Rev. Appl. Ent. 12, 1924, 39).

Forbes, W. T. M. 1923. The Lepidoptera of New York and Neighboring states. Cornell Univ., Agr. Exp. Sta. Memoir 68: 282.
Fyles, T. W. 1904. A new Gelechiid, *Trichotaphe levisella*, n. sp. Can. Ent. 36: 211.
Juillet, J. A. 1960. Immature stages, life histories, and behaviour of two hymenopterous parasites of the european pine shoot moth, *Rhyacionia buoliana* (Schiff.), (Lep., Olethreutidae). Can. Ent. 92: 342–346.
Muesebeck, C. F. W. 1918. Two important introduced parasites of the brown-tail moth. Jour. Agr. Res. 1465: 191–206.
———. 1924. A revision of the North American species of Ichneumon-flies belonging to the genus *Meteorus* Haliday. U. S. Nat. Mus. Proc. 63: 2, 2470, 1–44.
———. 1927. New species of chalcid flies parasitic on the gypsy-moth parasite, *Apanteles melanoscelus* (Ratz.). Jour. Agr. Res. 34: 4, 331–333 (*Dimmockia pallipes* Mues.).
———. 1935. On the genus *Oncophanes* Foerster, with descriptions of two new related genera. Ent. Soc. Amer. Ann. 28: 241–250.
———. 1958. Family Braconidae, p. 18–36, *in* Karl V. Krombein *et al.*, Hymenoptera of America North of Mexico. Synoptic Catalog (Agr. Monogr. 2, First Supplement), U.S.D.A., Washington, D.C. 305 p.
———. 1967. Family Braconidae, p. 27–60, *in* Karl V. Krombein, B. D. Burks, *et al.*, Hymenoptera of America north of Mexico. Synoptic Catalog (Agr. Monogr. No. 2, Second Supplement), U.S.D.A., Washington, D.C. 584 p.
———. 1967a. Three new reared Braconidae (Hymenoptera). Ent. News, 78, 5: 135–139.
———, and **L. M. Walkley.** 1951. Family Braconidae, p. 90–184 *in* C. F. W. Muesebeck *et al.*, Hymenoptera of America north of Mexico. Synoptic Catalog (Agr. Monogr. 2), U.S.D.A., Washington, D.C. 1420 p.
Simmonds, F. J. 1948. The biology of the parasites of *Loxostege sticticalis* Linn. in North America—*Meteorus loxostegei* Vier., (Braconidae, Meteorinae). Bull. Ent. Res. 38: 373–379.
Townes, Henry and **Marjorie Townes.** 1951. Family Ichneumonidae, p. 184–409, *in* C. F. W. Muesebeck *et al.*, Hymenoptera of America north of Mexico, Synoptic Catalog (Agr. Monogr. 2), U.S.D.A., Washington, D.C. 1420 p.